

## The Relation Between Hand Morphology and Quadrupedalism in Primates

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**ABSTRACT** Primate hands can be classified into two broad categories on the basis of ray proportions and other features. Ectaxonic hands are characterized by a longer fourth ray and are found in most strepsirhines. Most haplorhines possess mesaxonic hands which are characterized by a longer third ray. Preuschoft et al. ([1993] in H. Preuschoft and D.J. Chivers (eds.): *Hands of Primates*. Berlin: Springer-Verlag, pp. 21–30) proposed a biomechanical model which predicts that, during quadrupedalism, a mesaxonic hand should be held in a more neutral position with respect to the forearm, whereas an ectaxonic hand should be more ulnarly deviated.

The relation between hand positioning and the mesaxony/ectaxony categorization is investigated for 27 primate taxa. Videotapes were recorded for each species walking quadrupedally on arboreal supports. Several species were also videotaped during ground quadrupedalism. The degree of deviation of the hand relative to the substrate and the grips utilized were quantified for 18 species from the videotapes. Primates with mesaxonic hands use deviated hand positions and grips, especially when walking quadrupedally on small poles. Several species with ectaxonic hands use neutral hand positions and grips when walking quadrupedally on similar supports. Also, several primates, with either ectaxonic or mesaxonic hands, display a combination of deviated hand positions and grips when on arboreal substrates and neutral hand positioning when on the ground. The statistical results indicate that hand positioning during quadrupedal walking is more variable than expected based on the mesaxony/ectaxony classification. Furthermore, radiographic data suggest that primates evolved at least two different mechanisms of hand ulnar deviation. *Am J Phys Anthropol* 105:185–197, 1998. © 1998 Wiley-Liss, Inc.

A functional explanation of morphological features requires a documented relationship between form and usage. Recently, Preuschoft et al. (1993) have proposed specific structure-function relationships between hand anatomy and postures adopted during quadrupedalism in primates. In this report, we test these proposed relationships with kinematic data for an array of primate quadrupeds.

Two broad categories of primate hands have been defined on the basis of wrist

features, ray proportions, and intrinsic musculature (Jouffroy 1962, 1975; Jouffroy and Lessertisseur 1959, 1978, 1979; Jouffroy et

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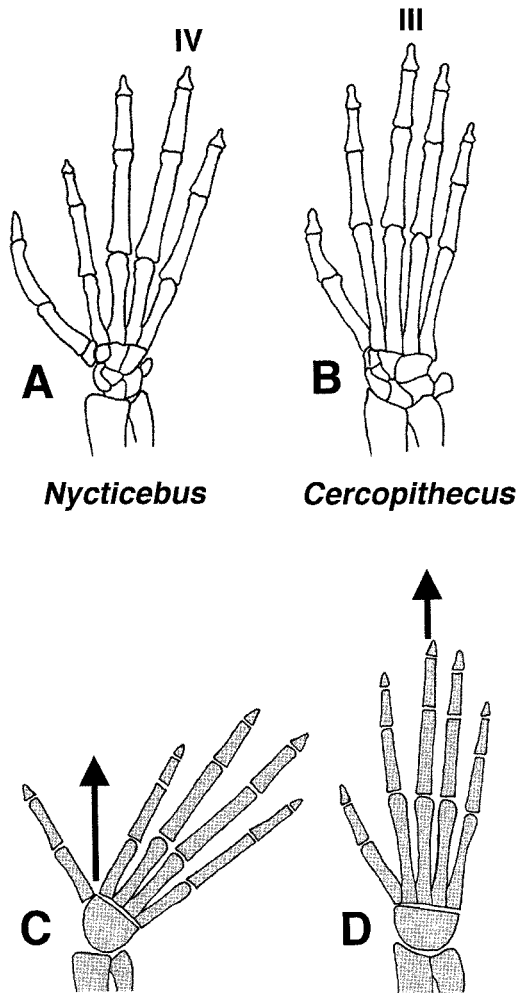


Fig. 1. Morphological and functional differences between ectaxonic (A,C) and mesaxonic (B,D) hands. In *Nycticebus* and most other strepsirrhines, ray IV is the longest, whereas in *Cercopithecus* and most other haplorhines ray III is the longest. According to the functional model (see Introduction), an ectaxonic hand displays a much larger degree of ulnar deviation, and the hand-substrate axis falls between rays I and II when gripping a support as represented by the arrow in C. In contrast, a mesaxonic hand is placed in a neutral position, and the hand-substrate axis falls along the third ray as represented by the arrow in D. The hand skeleton figures are adapted from Hershkovitz (1977).

al., 1991; Preuschoft et al. 1993). Ectaxonic hands are characterized by a longer fourth ray and are found in most strepsirrhines (Fig. 1). In contrast, mesaxonic hands are said to have a longer third ray and characterize most haplorhines (Fig. 1). Jouffroy et al. (1991) also defined a paraxonic hand, for

which rays III and IV are nearly equal in length. This type of hand is found in *Cheirogaleus*, *Varecia*, *Ateles*, *Lagothrix*, *Cercocebus*, and colobines (Jouffroy et al., 1991). Preuschoft et al. (1993) pointed out further that ectaxonic hands possess longer fingers and pollices, more developed ulnar carpal elements, and an extensive carpo-ulnar contact. In contrast, they described mesaxonic hands as having shorter fingers and pollices, more developed radial carpal elements, and a more reduced carpo-ulnar contact (Preuschoft et al., 1993). Their descriptions of wrist morphology along with the mesaxonic and ectaxonic hand categories have been questioned recently by Hamrick (1996b). Nonetheless, on the basis of ray proportions, primate hands can still be described as mesaxonic, ectaxonic, or paraxonic.

These reported differences in manual morphology among primates have been proposed to be related to differences in hand position during locomotion. Preuschoft et al. (1993) provided a biomechanical hypothesis to explain the morphological features associated with mesaxonic and ectaxonic hands. They suggested that during quadrupedalism a mesaxonic hand is placed in a neutral position. In this position, the long axis of the hand falls along the third ray when contacting the substrate (Fig. 1). In contrast, an ectaxonic hand displays a much larger degree of ulnar deviation. Consequently, the long axis of the hand with the substrate falls between rays I and II when gripping it (Fig. 1). Based on this analysis, Preuschoft and colleagues (1993) proposed that mesaxonic hands are indicative of habitual locomotion on large supports or the ground, whereas ectaxonic hands, best exemplified by the pincer grip of lorises according to the authors, are well suited for quadrupedal walking and climbing on rather thin branches.

The implications of this model are that terrestriality favors mesaxony while fine-branch locomotion favors ectaxony. Furthermore, this model implies that during quadrupedalism primates with mesaxonic hands maintain their hands in a more neutral position, whereas primates with ectaxonic hands display more deviated positions of the hand. Preuschoft and colleagues' (1993) functional hypotheses concerning manual mor-

TABLE 1. List of primate species examined in this study

Taxon	Hand category <sup>1</sup>	Number of individuals
<i>Microcebus murinus</i>	Ectaxonic	2
<i>Cheirogaleus medius</i>	Paraxonic	1
<i>Mirza coquereli</i>	Ectaxonic	2
<i>Otolemur garnettii</i>	Ectaxonic	2
<i>Perodicticus potto</i>	Ectaxonic	2
<i>Loris tardigradus</i>	Ectaxonic	1
<i>Nycticebus coucang</i>	Ectaxonic	1
<i>Eulemur fulvus</i>	Ectaxonic	2
<i>Eulemur mongoz</i>	Ectaxonic	1
<i>Varecia variegata</i>	Paraxonic	1
<i>Lemur catta</i>	Ectaxonic	1
<i>Hapalemur griseus</i>	Ectaxonic	1
<i>Saguinus midas</i>	Mesaxonic	2
<i>Saguinus oedipus</i>	Mesaxonic	2
<i>Saguinus fuscicollis</i>	Mesaxonic	2
<i>Callithrix jacchus</i>	Mesaxonic	2
<i>Callithrix geoffroyi</i>	Mesaxonic	2
<i>Saimiri sciureus</i>	Mesaxonic	2
<i>Cebus apella</i>	Mesaxonic	6
<i>Cebus albifrons</i>	Mesaxonic	1
<i>Ateles geoffroyi</i>	Paraxonic	1
<i>Cercopithecus aethiops</i>	Mesaxonic	3
<i>Erythrocebus patas</i>	Mesaxonic	1
<i>Papio anubis</i>	Mesaxonic	2
<i>Macaca fascicularis</i>	Mesaxonic	2
<i>Macaca mulatta</i>	Mesaxonic	3
<i>Macaca fuscata</i>	Mesaxonic	2

<sup>1</sup> Following Jouffroy et al. (1991).

phology and hand position during quadrupedalism are based primarily on behavioral data for *Loris tardigradus* (Nieschalk and Demes, 1993) and *Macaca mulatta* (Rawlins, 1993). In light of Bishop (1964), who reported considerable variability in the preferred orientations of the hand and substrate, we investigated whether these relationships between anatomy and behavior would be supported for a large sample of primates. Specifically, we wanted to know if hand positions adopted by primates during quadrupedalism would correlate with the mesaxony/ectaxony categorization.

## MATERIALS AND METHODS

We videotaped and quantified hand positions during arboreal and terrestrial quadrupedalism in 18 primate species with mesaxonic and ectaxonic hands (Table 1). We also videotaped nine haplorhines in their enclosures at the Bronx Zoo (New York), Central Park Zoo (New York), and Monkey Jungle (Florida) (Table 1). Although grips were not quantified for these primates, the axes of the hand with the support were noted (from lateral

or frontal camera views) and compared with those quantified for other species.

Six haplorhine species were studied in captivity at SUNY at Stony Brook using the methodology of Schmitt (1994, in press). Subjects were trained to walk within a plexiglass enclosure (6 m × 1 m × 1 m) along a wooden runway or a horizontal pole of 2.5 cm in diameter raised from the ground. The horizontal pole was PVC pipe coated with a nonslip surface of sand and white paint to provide a sharp contrast between the hand and substrate.

Twelve strepsirhine species were also studied in captivity at the Duke University Primate Center as part of a larger study on hand use (see Lemelin, 1996). Subjects were brought from their enclosures to an observation room (approximately 5 m × 6.5 m × 3 m) where natural supports of various dimensions and orientations were available. Only locomotor bouts on horizontal supports (less than 1 cm to 4 cm in diameter depending on the species) were considered in this study.

At SUNY-Stony Brook, subjects were filmed with an overhead camera view (superior view). This allowed us to quantify the angle of the hand relative to the substrate at touchdown (Fig. 2). Strepsirhine subjects studied at the Duke University Primate Center were filmed either with a lateral or frontal camera view. Because of constraints imposed by the animals and experimental setup, no overhead views were obtained for the subjects filmed at the Duke University Primate Center. For these primates, the axes of the hand with the substrate were quantified.

All animals were videotaped at 60 fields/s with videocameras (Panasonic WD-DW5000 or AG-450 Super VHS, Secaucus, NJ) equipped with electronic shutters (set between 1/125 and 1/1,000 s depending on light conditions) to reduce motion blur. All videotapes were viewed on a videocassette recorder (Panasonic AG-6300 or AG-7300, Secaucus, NJ) using the frame-by-frame playback option.

Hand positions during quadrupedalism were assessed using two different methodologies. For the haplorhine sample studied at SUNY-Stony Brook, we measured the angle formed between a line from the center of the

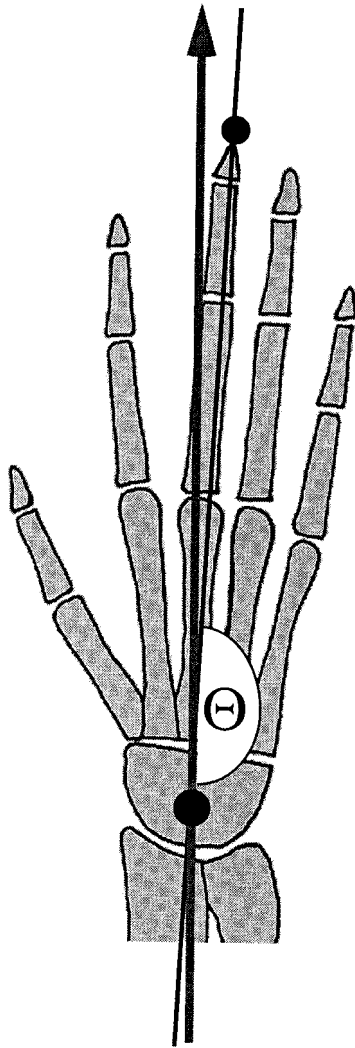


Fig. 2. Diagram of the hand-substrate angle as measured from a superior (dorsal) view for six haplorhine species. The arrow represents the long axis of the substrate (parallel with the line of travel) passing through the center of the wrist, and the black line is an axis passing through the center of the wrist and the tip of the third digit. The intersection of these two axes forms the hand-substrate angle ( $\theta$ ). This figure depicts a neutral hand position ( $\theta$  approximately  $175^\circ$ ). As the values of  $\theta$  decrease, the hand becomes more deviated.

wrist to the tip of the third digit and the substrate (Fig. 2). For the arboreal supports, this angle represents the orientation of the hand relative to the long axis of the pole. During ground quadrupedalism, this angle corresponds to the orientation of the hand relative to a line parallel to the path of the

animal. Hand-substrate angles were compared between the smallest poles the subjects would walk on and the ground using an analysis of covariance (ANCOVA) for which the speed of the animals was treated as the independent variable.

For the strepsirhine sample, the axes of the hand with the substrate were quantified. A grip was defined as a single event in which the hand was in contact with the support. A new grip was recorded every time the hand touched down during a locomotor cycle. The axis of the hand with the support refers to the alignment of the digits when gripping a horizontal support or the line of travel when on the ground. For example, a 2-3 hand-substrate axis means that the support fell between the second and third digits for a given grip.

Grips were quantified for arboreal supports of different sizes and the ground (in *Lemur catta* only). The preference for a particular grip within taxa was tested using the *G*-test for goodness of fit (single classification; expected frequencies based on a binomial distribution) with the Williams' correction factor (Sokal and Rohlf, 1981).

The primate species under investigation were classified into three hand-position categories according to the degree of deviation of the hand relative to the substrate or the grips used during quadrupedalism.<sup>1</sup> Primates falling into the deviated category used most commonly grips with 1-2 or along 2 hand-substrate axes, without preference for either axis. The intermediate category was assigned to primates relying on grips with 1-2, along 2, and 2-3 hand-substrate axes, with either a preference for the along 2 axis or no preference for all three axes. Finally, primates falling into the neutral category used grips with 2-3, along 3, or 3-4 hand-substrate axes, with or without preference for one of these axes.

In order to understand further the mechanism of ulnar deviation, we radiographed

<sup>1</sup>Hand-substrate axes and hand-substrate angles are equivalent measures of hand positioning. Our assessment of the relationship between angular measures and grip counts in the six haplorhines studied with overhead camera views revealed that hand-substrate angles lower than  $150^\circ$  corresponded to 1-2 hand-substrate axes or axes falling along the thumb. For hand-substrate angles above  $160^\circ$ , 2-3 hand-substrate axes were most common.

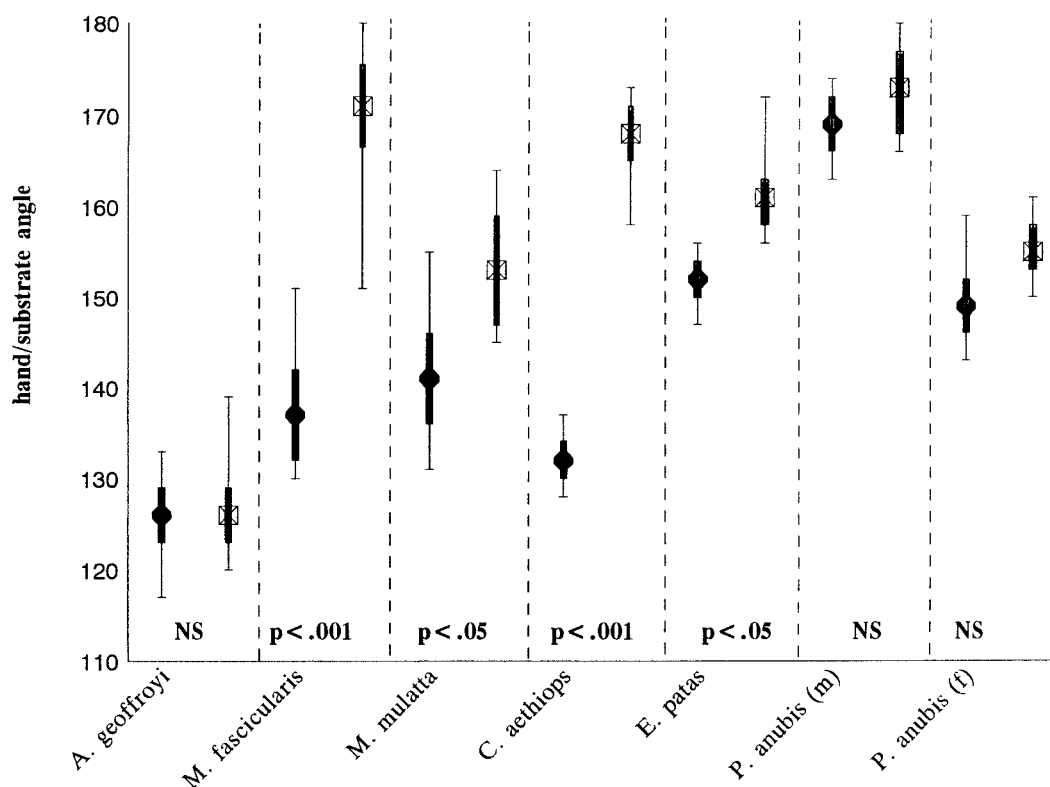


Fig. 3. Hand-substrate angles for six haplorhine species during quadrupedalism on smallest poles (black diamonds) and ground (open squares). The symbols represent the speed-adjusted (adjusted-y) means, the rectangles one standard error of the adjusted-y mean,

and the whiskers the range. The results of the significance tests for the ANCOVAs between the smallest poles and ground are listed for each taxon. Only the male and female *P. anubis* subjects were treated separately because significant differences were found between sexes.

anesthetized subjects of *Cercopithecus aethiops* ( $n = 2$ ), *Macaca fascicularis* ( $n = 2$ ), *Papio anubis* ( $n = 1$ ), and *Nycticebus coucang* ( $n = 1$ ) while manipulating the hand. For each subject, one radiograph was taken with the hand in a neutral position and one with the hand ulnarly deviated until no further deviation could be achieved.

### RESULTS

During quadrupedalism on poles, deviated hand positions were the norm for the six haplorhine species studied at SUNY-Stony Brook despite their mesaxonic hand anatomy. For all species, the hand was more deviated relative to the substrate while walking quadrupedally on small poles than on the ground. These differences in hand positioning are evinced by the smaller hand-substrate angles observed for the small poles

(Fig. 3). Differences in hand-substrate angles for the small poles vs. ground were significant for all species except *Ateles geoffroyi* and *P. anubis* (Fig. 3).

Clearly, primates with mesaxonic or paraxonic (i.e., *Ateles*) hands are capable of using a wide range of hand positions that appear to vary according to substrate differences. The primate species in Figure 3 are arranged according to their degree of arboreality. It is interesting to note that the most arboreal species, *A. geoffroyi* (Cant, 1986; Mittermeier, 1978; Richard, 1970), has the most deviated hand positions on both small poles and ground. *A. geoffroyi* is followed by *M. fascicularis*, a highly arboreal macaque (Cant, 1988; Rodman, 1979), the semiterrestrial (sensu Ripley, 1977) *Macaca mulatta* and *C. aethiops* (Rawlins, 1993; Rose, 1979), and the highly terrestrial *Erythrocebus pa-*



*tas* and *P. anubis* (Rose, 1973, 1977). This gradient of deviated/more neutral hand positions follows closely substrate preferences for these taxa in their natural habitats.

As with the haplorhines, the strepsirhines examined in this study showed variability in hand axes with the substrate that did not always follow the expectations of the mesaxonic/ectaxonic dichotomy. For example, cheirogaleids, which are characterized by paraxonic or ectaxonic hands, used neutral hand positions. *Microcebus murinus* used preferentially grips with a 2-3 hand-substrate axis ( $G(\text{Williams})$ ,  $P < 0.01$ ) (Figs. 4, 5). *Cheirogaleus medius* and *Mirza coquereli* relied on grips with 2-3 or along 3 hand-substrate axes (Fig. 4). These observations for cheirogaleids are similar to those figured in Cartmill (1974).

*Lemur catta*, another primate with ectaxonic hands, displayed neutral hand positions when walking quadrupedally on the ground, with the axis of the hand and the line of travel falling between digits III and IV (Fig. 4). However, during arboreal quadrupedalism, the hand of *L. catta* shifted toward deviated positions characterized by grips with 1-2 or along 2 hand-substrate axes (Fig. 4). Less deviated hand positions were observed in *Eulemur fulvus* and *Eulemur mongoz* on arboreal supports, with no preference for grips with hand-substrate axes falling along digit II or on either side of it (1-2 or 2-3 hand-substrate axes) for the former (Figs. 4, 5) and a preference for grips along 2 hand-substrate axes for the latter ( $G(\text{Williams})$ ,  $P < 0.01$ ) (Fig. 4). Similarly, *Otolemur garnettii* and *Hapalemur griseus* showed less deviated hand positions, with a preference for grips with along 2 hand-substrate axes ( $G(\text{Williams})$ ,  $P < 0.01$ ) (Fig. 4).

Lorisids have been described as having pincer-like hands (Biegert, 1963; Forster, 1933, 1934; Jouffroy, 1962, 1993; Preuschoft et al., 1993) because of the very short second digit relative to the fourth one (Jouffroy and Lessertisseur, 1977, 1979; Jouffroy et al., 1991) and the very divergent first carpometacarpal joint relative to the second carpometacarpal facet (Hamrick, 1996d). *Perodicticus potto*, *Loris tardigradus*, and *N. coucang* used deviated hand positions (grips with 1-2

or along 2 hand-substrate axes, with no preference for either one axis) (Figs. 4, 5).

Compared to other strepsirhines with ectaxonic or paraxonic hands, *Varecia variegata* displayed a strong preference for grips with 1-2 hand-substrate axes ( $G(\text{Williams})$ ,  $P < 0.01$ ). However, we noticed in both lateral and frontal views that the forearm and hand of *Varecia* were more supinated when gripping an arboreal support compared to other closely related taxa (i.e., *Eulemur*; *L. catta*, and *H. griseus*). As a result, the hand (mainly the palm) contacted the lateral side of the support instead of the top as in other lemurids. In addition, the forearm and hand were aligned (i.e., more neutral position) during most of the support phase of a quadrupedal step. Such hand position of *Varecia* during quadrupedalism is figured in Fleagle and Anapol (1992) and has been described by Rose (personal communication) as a thumb-hook grip.

Videotapes of several species of *Saguinus* and *Callithrix*, *Saimiri sciureus*, *Cebus apella*, *Cebus albifrons*, and *Macaca fuscata* in zoological enclosures revealed similar patterns as found for the primates discussed above. Both *Cebus* species used deviated hand positions on arboreal supports, whereas *Saimiri* relied on intermediate hand positions on similar supports. On the ground, *C. apella* and *M. fuscata* displayed neutral hand positions. All callitrichids observed in this study used neutral hand positions on arboreal supports similar to those observed for cheirogaleids. Similar observations have been reported for *Callithrix jacchus* (Rothe, 1972) and some didelphid marsupials (Cartmill, 1974; Lemelin, 1996). Interestingly, *Leontopithecus*, a callitrichid with relatively longer hands (Jouffroy et al., 1991), relies heavily on deviated hand positions during quadrupedal walking and running on arboreal supports (Rosenberger and Stafford, 1994; Stafford et al., 1996).

Manipulations of the hand of anesthetized subjects revealed two very different mechanisms of ulnar deviation in primates. When the pronated hand of *N. coucang* was brought from a neutral to a more ulnarly deviated position, notable movement occurred at the antebrachio-carpal and midcarpal joints (Fig. 6). The same manipulation of

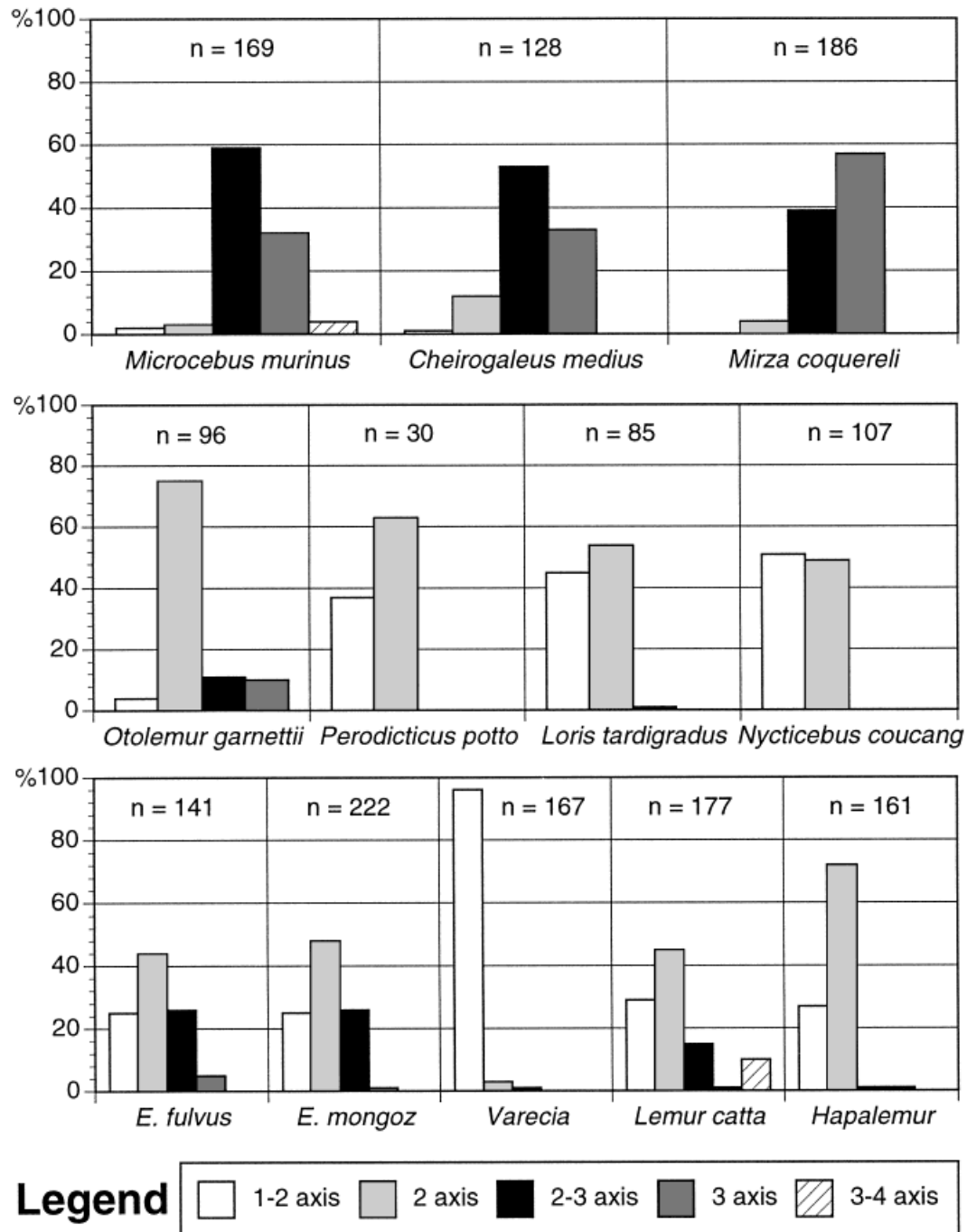


Fig. 4. Relative frequencies of grips used during pronograde quadrupedalism in 12 strepsirhine species. The n refers to the total number of grips observed for each taxon. A 1-2 axis indicates a grip for which the support fell between the first and second digit.

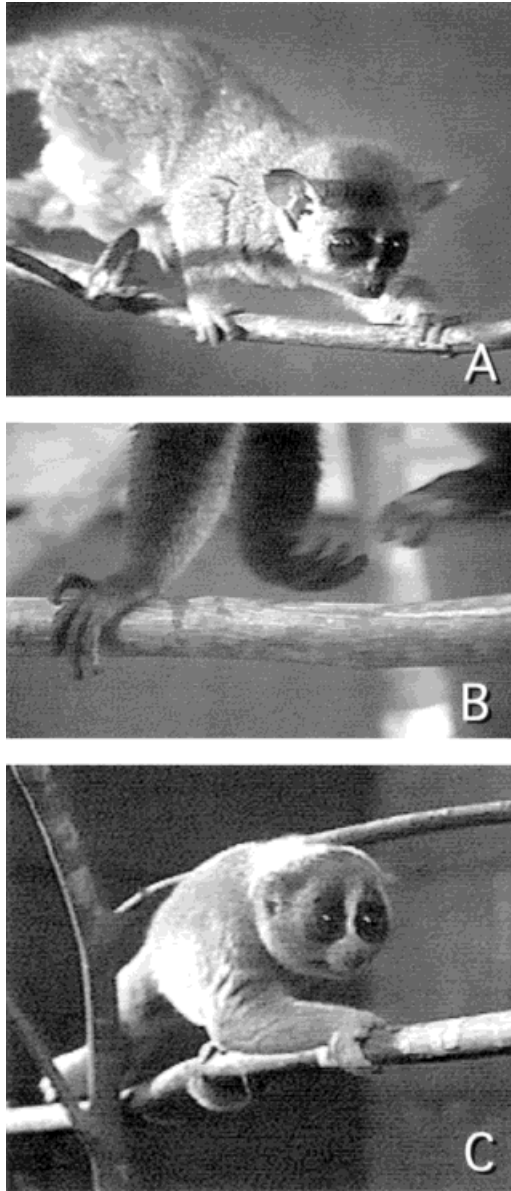


Fig. 5. Single video frames of hand position during a quadrupedal step in *Microcebus murinus* (A) (the axis of the hand with the horizontal support less than 1 cm in diameter falls between digits II and III), *Eulemur fulvus* (B) (the axis of the hand with the 2–3 cm diameter support falls along digit II), and *Nycticebus coucang* (C) (the axis of the hand with the 2–3 cm diameter support falls between digits I and II).

the hand in *M. fascicularis*, *C. aethiops*, and *P. anubis* produced less ulnar deviation at the antebrachicarpal and midcarpal joints. Compared to the slow loris, the flatter articular surfaces of the hamate and capitate onto

the triquetrum promoted less movement, especially in *C. aethiops* and *P. anubis*, and the prominent ulnar styloid process impacting onto the triquetrum and pisiform restricted ulnar deviation of the hand (Fig. 6). Instead, ulnar deviation was achieved mainly at the metacarpophalangeal joints of rays II–V (Fig. 6).

## DISCUSSION

We have attempted to evaluate behavioral predictions concerning hand position during quadrupedal locomotion on the basis of morphological features of the wrist and ray proportions of primate hands. We expected that primates characterized by ectaxonic hands would grip supports using more deviated positions. Conversely, we expected that primates with mesaxonic hands would adopt neutral (i.e., nondeviated) hand positions when gripping arboreal substrates or walking quadrupedally on the ground. Our results, summarized in Table 2, which includes observations from zoo animals as well, indicate that hand positioning during quadrupedal walking is much more variable than what we expected on the basis of the model presented above. The presence of a mesaxonic or ectaxonic hand does not necessarily imply deviated or neutral hand positions.

The results of this study evince one important fact: many primates with mesaxonic hands regularly adopt deviated hand positions, and several others with ectaxonic hands regularly adopt neutral hand positions. The relationship between ectaxy/mesaxy and deviated/neutral hand positions, although found to be true for several species, does not apply for many primates we investigated. For example, *L. catta*, a lemur with ectaxonic hands, spends about 65% of its time on the ground while traveling (Sussman, 1974; Ward and Sussman, 1979). On the ground, *L. catta* uses neutral hand positions, but, when walking quadrupedally on arboreal substrates, it relies on deviated hand positions. Similarly, *M. fascicularis*, an Old World monkey with mesaxonic hands, is highly arboreal (Cant, 1988; Rodman, 1979) and uses deviated hand positions when walking quadrupedally on small-diameter poles.





Fig. 6. Roentgenograms (x-rays) of the hand of anesthetized specimens of *Nycticebus coucang* (A,B) and *Cercopithecus aethiops* (C,D). Upon ulnar deviation of the prone hand of *N. coucang* (A), most of the movement occurs at the antebrachiocarpal and midcarpal joints

(B). The same manipulation of the prone hand of *C. aethiops* (C) produces more movement at the metacarpophalangeal joints of rays II-V (D). Note also the broad ulnocarpal contact in *C. aethiops* indicated by the arrow (D) compared to that of *N. coucang*. Scale bars = 2 cm.

The fact that we did not find a clearcut correspondence between mesaxony/ectaxony and hand positioning suggests to us that the behavioral predictions made by Preuschoft

et al. (1993) mainly on the basis of ray proportions are not valid. In other words, a mesaxonic hand may not be constrained to a single behavioral pattern, such as a neutral

TABLE 2. Summary table of hand positioning based on hand-substrate angles and/or grips for primate species examined in this study<sup>1</sup>

Hand category/position	Deviated	Intermediate	Neutral
Ectaxonic	<i>L. tardigradus</i> (p) <i>N. coucang</i> (p) <i>P. potto</i> (p) <i>L. catta</i> (p)	<i>E. fulvus</i> (p) <i>E. mongoz</i> (p) <i>O. garnettii</i> (p) <i>H. griseus</i> (p)	<i>M. murinus</i> (p) <i>M. coquereli</i> (p) <i>L. catta</i> (g)
Paraxonic	<i>A. geoffroyi</i> (p, g) <i>M. fascicularis</i> (p)	<i>S. sciureus</i> (p)	<i>C. medius</i> (p) <i>S. midas</i> (p)
Mesaxonic	<i>M. mulatta</i> (p) <i>C. aethiops</i> (p) <i>E. patas</i> (p) <i>P. anubis</i> (f) (p) <i>C. apella</i> (p) <i>C. albifrons</i> (p)	<i>M. mulatta</i> (g) <i>E. patas</i> (g) <i>P. anubis</i> (f) (g)	<i>S. oedipus</i> (p) <i>S. fuscicollis</i> (p) <i>C. jacchus</i> (p) <i>C. geoffroyi</i> (p) <i>C. apella</i> (g) <i>M. fascicularis</i> (g) <i>M. fuscata</i> (g) <i>C. aethiops</i> (g) <i>P. anubis</i> (m) (p, g)

<sup>1</sup> *Varecia* was omitted from this summary table because of its peculiar hand positioning (see Results). f, female; g, ground; m, male; p, poles or branches.

hand position, but to a range of behaviors, including neutral and more deviated hand positions.

Despite the poor correlation between ray proportions (from which the mesaxonic/ectaxonic categorization is based) and hand positioning, other morphological features of the hand may be more diagnostic to explain the behavioral differences observed in this study. Our data show that many primates use deviated hand positions when walking quadrupedally on arboreal supports. The radiographic data presented above indicate that ulnar deviation of the hand can be achieved mainly at the wrist in one lorisid or at the metacarpophalangeal joints in several cercopithecoids.

Several studies have pointed out how the shape of the carpal joints can affect the range of movements of the hand during locomotion and posture in primates (Cartmill and Milton, 1977; Fleagle, 1977; Hamrick, 1996a,c,d; Jenkins, 1981; Jenkins and Fleagle, 1975; Lewis, 1974, 1985a,b; O'Connor, 1975; Sarmiento, 1988; Yalden, 1972; Ziemer, 1978). Specifically, the degree of midcarpal curvature is correlated with the range of radioulnar deviation and midcarpal rotation of the hand (Hamrick, 1996a,c,d; Jenkins, 1981; Jenkins and Fleagle, 1975; Sarmiento, 1988).

Compared to other quadrupedal primates, the lorisid proximal joint facets of the capitate and hamate are more curved, and the hamate spiral facet is orientated more dor-

sally (Forster, 1933, 1934; Hamrick, 1996a,d; Lewis, 1985a). This morphology promotes pronation accompanied with extreme ulnar deviation of the hand (Hamrick, 1996a,d; Lewis, 1985a) as well as supination (personal observations). In contrast to other primate quadrupeds, lorisids rely heavily on deliberate climbing and bridging (Charles-Dominique, 1971, 1974, 1977; Dykyj, 1980; Glassman and Wells, 1984; Ishida et al., 1983; Oxnard et al., 1990; Walker, 1974, 1979).

The condition seen in the lorisid midcarpal joint resembles that reported by Jenkins (1981) for arm-swinging primates like *Ateles* and *Hylobates*. The half "ball-and-socket" midcarpal joint of *Ateles* and *Hylobates* allows considerable supination of the hand during the support phase of arm swinging (Jenkins, 1981). Moreover, several features of the distal radioulnar and antebrachio-carpal joints of lorisids parallel those of hominoids, including a reduced ulnar styloid process (Cartmill and Milton, 1977).

These differences in carpal joint morphology are somewhat consistent with our results on hand positioning and hand manipulation of anesthetized primate subjects. Within our strepsirrhine sample, deviated hand positions as reflected by the preferred hand-support axes were found consistently in all three lorisids. Accordingly, the midcarpal joint of lorisids is designed to allow extreme ulnar deviation of the hand as demonstrated above (Fig. 6). Within our

haplorhine sample, *Ateles* showed the most deviated hand positions, as reflected by the significantly lower hand-substrate angles. Compared to Old World monkeys, the midcarpal joint of the spider monkey is designed to allow more rotation (Jenkins, 1981). Although midcarpal supination occurs during arm swinging in *Ateles* (Jenkins, 1981), it is likely that the same midcarpal joint morphology allows also considerable ulnar deviation when the hand is pronated.

Several primates other than lorises and *Ateles* also exhibited deviated hand positions on arboreal substrates. However, *L. catta*, *M. fascicularis*, *C. aethiops*, *E. patas*, and *P. anubis* possess flatter midcarpal joint facets (Hamrick, 1996a,c,d; O'Connor, 1975; Sarmiento, 1988; Yalden, 1972; personal observations) that should allow less ulnar deviation. In several cercopithecoids, ulnar deviation is achieved primarily at the metacarpophalangeal joints of the fingers (Fig. 6). This particular mechanism of ulnar deviation of the hand is especially marked in the more terrestrially adapted species like *C. aethiops* and *P. anubis*, is very different from that of *N. coucang*, and may be reflected in the architecture of the metacarpophalangeal joints.

This evidence suggests that at least two different mechanisms of ulnar deviation of the hand may be present in primates. Furthermore, this evidence underlines the complex and integrated nature of the hand as a locomotor organ and the need for fine-grained, more detailed anatomical/behavioral studies.

### SUMMARY AND CONCLUSIONS

Proposed relationships between anatomy and behavior based on morphological data must be tested with kinematic data from living animals. In this paper, we tested the proposal of Preuschoft et al. (1993) that primates with ectaxonic hands would use more deviated hand positions and that primates with mesaxonic hands would use more neutral hand positions. We videorecorded hand positions during quadrupedalism on arboreal and terrestrial supports for a large sample of primates.

No clearcut relationship was found between these hand categories based on ray

proportions and hand kinematics. Many primates were capable of adopting both neutral and deviated hand positions regardless of hand category, although there was a tendency for individuals to adopt more deviated positions on arboreal supports. This evidence suggests that hand kinematics is adjusted according to the substrate rather than being constrained by the anatomy. Also, differences in how ulnar deviation was achieved (either at the midcarpal joint or at the metacarpophalangeal joints) reflected an intriguing phylogenetic signal that separated lorises and cercopithecoids.

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